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TERMINAL EGG NEGLECT IN THE AMERICAN WHITE PELICAN

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ABSTRACT.—Brood reduction theory suggests that parents may allocate less care to their youngest, or terminal offspring because it has a lower potential reproductive value. The possibility that American White Pelicans (*Pelecanus erythrorhynchos*), which exhibit hatch asynchrony and a high probability of brood reduction, selectively neglect their terminal, or b-egg was examined by monitoring temperatures of artificial eggs. Before the onset of pipping, mean upper egg surface temperatures exceeded 37°C, and individual readings rarely fell below 36.0°C. After pipping of the a-egg, upper egg surface temperatures of the remaining (artificial) b-egg dropped significantly, and more individual readings fell below 36.0°C. A temperature gradient between egg top and bottom was present before pipping, but not subsequently. These results, along with evidence from a separate study indicating that hatching of pelican embryos is significantly retarded by moderate chilling, suggest that there is a potential for biologically relevant neglect of the terminal egg after pipping of the first egg in this species. *Received 24 Oct. 1989, accepted 1 Feb. 1990.*

There is growing evidence that incubation of the last egg to hatch in asynchronously hatching clutches of some ground nesting species may become disrupted as parents begin to tend to the needs of the first pipped or hatched members of the brood. Neglect of terminal eggs has been documented primarily in gulls and terns (Laridae) (Beer 1962, Drent 1970, Haycock and Threlfall 1975, Courtney 1979), and has been noted or suspected in some other species, including the American Coot (*Fulica americana,* Gullion 1954), South Polar Skua (*Catharacta maccormicki,* Spellerberg 1971), and Pied-billed Grebe (*Podilymbus podiceps,* Forbes and Ankney 1988). Although a quantitative theoretical treatment of terminal egg neglect is lacking, it is plausible that neglect is most prevalent in species that are known to exhibit brood reduction. Where loss of an offspring through the brood reduction process is likely, parents may be able to increase their own fitness by investing relatively less in the potential victim (Mock 1987), usually the last young hatched. Incubation neglect of the last-hatched egg by parents that are actively feeding or otherwise caring for older siblings can be viewed as a manifestation of differential parental care extending back into the late incubation period.

In the American White Pelican (*Pelecanus erythrorhynchos*), brood reduction affecting primarily the younger of the two siblings is virtually obligate (Cash and Evans 1986). Hatching asynchrony in this species

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averages about 2.5 days. When the first, or a-egg pips, its vocalizations cause the incubating parent to shuffle its webbed feet off the eggs (pelicans lack a brood patch and normally incubate eggs under the foot webs). Eggs are then pushed back between the legs for the remainder of the incubation period (Evans 1988a, 1989). At this time the eggs, no longer held in position by the parent's foot webs, are subject to exposure whenever the parent rises to preen or when it settles without covering a partially dislodged egg. Exposure is especially likely for the b-egg after the a-egg has hatched. Using temperature sensors implanted at the center of artificial eggs, I found (Evans 1989) that as a result of such exposure, the terminal b-egg was subjected to increasing variability and lower ranges in temperature as the hatch progressed, but mean core temperature was unaffected.

The above results provide conflicting evidence for terminal egg neglect in white pelicans: observations of increased egg exposure and the lower range of temperature of b-eggs after the a-egg pips suggest neglect, but the more stable mean core temperatures do not. To further examine the problem of terminal egg neglect in this species, I did preliminary tests (reported fully below) where I positioned a temperature probe on the upper surface of an artificial egg that was immovably fixed in position near the center of the nest. Before the onset of pipping of the companion a-egg, mean egg temperature recorded from this probe was higher than any of the mean temperatures previously reported for this species when probes were positioned at the egg center. After the companion a-egg pipped, upper surface temperatures fell back to a level similar to those previously obtained from the egg center, a result consistent with the terminal egg neglect hypothesis. These results also suggested the hypothesis that the temperature gradient, normally expected between top and bottom of a large egg (Drent 1970), may be less pronounced or even absent when incubation behavior changes upon pipping of the first egg. The objective of this study was to obtain additional egg temperature measurements to permit a closer examination of these hypotheses.

METHODS

Pelicans were studied at a colony of about 2600 nests (1989 census) at East Shoal Lake, Manitoba, Canada. Observations of courtship flights in April were used to predict the approximate date of hatching (Evans and Cash 1985), so that brief visits to the colony to install instrumented eggs could be delayed until the earliest nests were in the late stages of incubation, when the risk of desertion due to human disturbance is minimal. It was found that disturbance could be further decreased by making the final approach, of about 50 m, slowly on hands and knees.

All egg temperatures were taken from artificial eggs consisting of a natural pelican egg shell strengthened internally with a thin layer of fiberglass and filled with agar. These eggs have weight and thermal characteristics similar to fresh eggs (Evans 1989). In the preliminary

experiment, artificial eggs were fixed in position by inserting and gluing a wire, 10 cm in length, down from the bottom of the egg. When the protruding wire was pushed into the bottom of the nest, egg shifting or turning could not occur. For this data set, a thermistor bead probe, about 1 mm in diameter, was affixed with transparent tape to the upper surface of the egg approximately 2 cm towards the blunt end from the position of maximum diameter around the long axis of the egg. This probe location approximated the location of the pip hole in natural eggs. The lead from the probe was taken under the egg and thence under the nest rim and across the ground to a weatherproof instrument box located outside the limits of the colony, about 30 m from the nest being measured. Temperatures in this experiment were recorded every 5 or 10 min with a calibrated (±0.2°C) model SQ 2 4-channel data logger (Grant Instruments, Cambridge), with up to four different nests being monitored simultaneously. A total of 20 nests, 10 before pipping and 10 during and after hatching of the a-egg were measured. For the nests monitored during and after the a-egg hatched, it was found that the parents accepted the fixed eggs without problem provided they were put in position before the a-egg had actually hatched. Data reported here were for nests set up with late stage a-pip eggs that had always hatched before termination of data collection the next day.

In an attempt to make the eggs used for temperature measurements more natural, eggs used in the main experiment were not fixed in position. During their construction, a 16 g lead weight was glued to the inside of the shell to ensure a weight asymmetry. As described by Drent (1970) for natural eggs, weight asymmetry combined with parental billing of the egg during egg "turning" acts to ensure that the heavy side of the egg is usually downwards in the nest. These eggs were equipped with four temperature sensors, each consisting of a 30 ga Type T teflon-coated thermocouple wire with soldered tip covered by a bead of epoxy. Three independent sensors were implanted flush with the outer surface of the egg shell. As in the preliminary experiment each was approximately 2 cm towards the blunt end as measured from a circle around the point of maximum diameter on the longitudinal axis of the egg. These probes were positioned so that when the egg lay flat in the nest, heavy side down, one probe was up (0°), one down (180°), and one at the side (90°). A fourth probe was positioned at the center of the egg, to detect internally the presence of a gradient, if any, between top and bottom. The leads from each of the sensory beads proceeded into the egg, and thence out by a common hole drilled through the bottom, well away from the lower surface temperature sensor. Outside the egg, the four leads were taped into a single composite wire which exited through the nest bottom and out below the nest rim, leaving the egg essentially free to be moved about within the nest. Beyond the nest, thermocouple leads were tied to an embedded spike to ensure walking pelicans would not inadvertently pull the artificial eggs from the nest. Leads then continued on the surface of the ground to the instrument box as described above. Temperature measurements for the main experiment were recorded automatically every 5 min with a calibrated (±0.1°C) SQ 1203 8-channel data logger. The use of all 8 channels in this experiment made it possible to monitor simultaneously all probes from two eggs in different nests. Ten nests, two per day for five days, were monitored at each of three stages of incubation: (1) before pipping, when eggs were incubated under the foot webs, (2) after pipping of the a-egg, when the eggs were no longer held under the foot webs, and (3) after hatching of a-egg. No instances of rejection or failure to incubate the artificial eggs occurred at any stage.

Experimental protocol was similar for both experiments. At each nest, one egg was temporarily removed and replaced with the instrumented artificial egg. The usual routine was to enter the colony in the morning, turn off the data loggers, and verify that the probes and appropriate nest contents were in place. In the preliminary experiment, I then left the colony to download the data to a portable microcomputer, then repositioned the probes at new

nests upon returning about 2 h later. In the main experiment, probes were usually repositioned before leaving the colony to download, so that it was not necessary to enter the colony or cause any incubating pelicans to leave their nests when returning to reset the data loggers for the next run. Rare exceptions to this routine occurred when observations with binoculars or monitoring of current egg temperature indicated a problem with the nest contents that required correcting. In one instance, rain precluded normal nest checks, and the equipment was left in place for two days. Only the first day of data was used in analyses.

To reduce possible effects of my presence on egg temperatures and to ensure central egg temperatures had time to reach a steady state (Evans 1989), the first three hours of data and any readings logged after my arrival at the colony the next day were excluded from analysis. Readings were analysed for an average of 19.3 ± 0.6 h/nest in the preliminary experiment and for 16.0 ± 0.5 h/nest in the second. Descriptive statistics were computed for the readings for each probe from each nest. The means were then treated as single data points and subjected to higher order analyses following the computational methods of Bruning and Kintz (1968). Additional non-parametric tests, when needed for data sets that were non-normal, were done according to Daniel (1978).

RESULTS

Fixed eggs.—Before the onset of pipping, the overall mean upper surface temperature derived from the 10 individual means of the fixed artificial eggs was 37.4 ± 0.2 (SE) °C (average of 161 readings/nest), significantly warmer ($t = 5.87$, df = 18, $P < 0.001$) than the upper egg surface during and after the hatching of the a-egg (34.6 ± 0.4°C, 185 readings/nest).

To provide further insight into the possibility of egg neglect as the hatch progressed, the proportion of temperature readings equal to or greater than 36.0°C were also calculated for each nest. This particular temperature was chosen for analysis on the basis of incubator studies (Evans 1990) indicating that hatching of pelican eggs can be significantly retarded when pipped eggs are incubated at 33.0°C, but are not affected relative to controls when incubated at 36.0°C. The exact temperature between these two values where hatch retardation begins has not been determined. For present purposes, it was assumed that the relative proportions of readings above or below 36.0°C at a nest provides an estimate of the potential for biologically significant egg neglect. Before pipping, the median proportion of temperature readings per nest that was equal to or greater than 36.0°C was 89.9%, significantly greater (Mann-Whitney $U = 1$, $N_1 = N_2 = 10$, $P < 0.001$) than the median proportion of 22.0% achieved during and after the hatching of the a-egg.

Movable eggs.—Before the onset of pipping the overall average of the 10 nest means for the upper surface probes in movable artificial eggs was 37.2°C, essentially identical to the mean temperature obtained for the same incubation stage and probe location in the fixed eggs described above. Mean upper surface temperature of the artificial b-egg then dropped

TABLE 1
MEAN EGG TEMPERATURES FOR THREE PROBE LOCATIONS OVER THREE STAGES OF INCUBATION

Incubation stage[a] (mean readings/nest)	Probe location			*F*	*P*
	Top surface	Egg center	Bottom surface		
pre-pip (200)	37.2 ± 0.1	35.7 ± 0.2	34.8 ± 0.3	34.62	<0.001
a-pip (184)	35.6 ± 0.3	35.8 ± 0.3	35.9 ± 0.3	1.25	NS[b]
a-hatch (192)	35.0 ± 0.4	35.5 ± 0.2	35.3 ± 0.4	2.48	NS
F	13.75	2.62	0.37		
P	<0.001	NS	NS		

[a] Pre-pip = neither egg yet pipped; a-pip = a-egg pipped, b-egg not pipped; a-hatch = a-egg hatched, b-egg not yet pipped.
[b] NS = $P > 0.05$, N = 10 nests at each stage.

significantly when the a-egg pipped and hatched (Table 1). Egg center and bottom surface temperatures did not differ significantly.

Overall comparisons of egg temperatures among the top, bottom, and centrally located probes for all three incubation stages (pre-pip, a-egg pipped, a-egg hatched) were significant for probe position (two-way ANOVA, repeated measures on probe location, $F = 6.54$, df = 2,54, $P < 0.005$) and for interaction between probe position and incubation stage ($F = 19.33$, df = 4,54, $P < 0.001$). There was a definite temperature gradient through the egg from top to bottom during the pre-pip stage of incubation (Table 1). This temperature gradient was no longer present after the onset of pipping, when all probe locations took on mean readings between 35.0 and 35.9°C. The proportion of readings greater than or equal to 36.0°C followed a pattern similar to mean temperature (Table 2). Over 92% of readings equalled or exceeded 36.0°C on the upper egg surface during the pre-pip stage, while all other probes and stages were significantly lower.

Temperatures recorded by the probe located on the egg surface midway (90°) between the upper and lower probes did not differ significantly from those recorded from the egg center ($P > 0.05$). Mean temperatures for the 90° probe were: pre-pip = 35.8 ± 0.3, a-pip = 35.9 ± 0.3, a-hatch = 35.0 ± 0.4°C (compare to values for egg center, Table 1). During the pre-pip incubation period, the 90° surface probe did not track either the warmed upper surface or the cooler lower surface, but rather maintained an intermediate position within the gradient between top and bottom as did the center of the egg itself. Analysis of the magnitude of the pre-pip temperature gradient (temperature of upper minus lower probe) during successive 3-h periods between 1700 and 0800 h CDT indicated no sig-

TABLE 2

MEDIAN PROPORTION OF EGG TEMPERATURE READINGS ≥ 36.0°C FOR THREE PROBE LOCATIONS OVER THREE STAGES OF INCUBATION

Incubation stage[a]	Probe location			Chi-square[b]	*P*
	Top surface	Egg center	Bottom surface		
pre-pip	92.1	47.8	26.7	15.20	<0.001
a-pip	49.5	51.6	51.6	3.05	NS[c]
a-hatch	32.5	21.8	37.6	3.80	NS
H[d]	13.80	0.65	5.95		
P	<0.001	NS	NS		

[a] See footnote[a], Table 1.

[b] Comparison among probe locations for each incubation stage, Friedman's ANOVA by ranks, df = 2, N = 10 for each probe location.

[c] NS = $P > 0.05$.

[d] Comparison among incubation stages for each probe location, Kruskall-Wallis test, H distributed approximately as Chi-square, df = 2, N = 10 for each incubation stage.

nificant changes in relation to time of day (one-way ANOVA, repeat measures, $F = 0.7$, $P > 0.05$).

DISCUSSION

Results of both experiments show that the upper surface temperature of American White Pelican eggs is held at a relatively stable temperature of just over 37.0°C prior to the onset of pipping. Essentially identical results by the two different methods, employing fixed eggs and movable but weighted eggs, lends support to the conclusion that this temperature represents the actual biological temperature regimen applied to eggs by pelicans, at least during the latter portions of the pre-pipping incubation period when these measurements were taken. Because embryos were absent from the instrumented eggs, the upper surface temperature can be taken as that applied by the incubating parent independent of heat production and vocal feedback from the embryos. Mean incubation temperatures above 37°C are rare among birds (Webb 1987), and could indicate that pelican embryos are particularly sensitive to cooling.

Temperatures in the region of 35°C obtained for probes located at the egg center in this study are in close agreement with those reported for the same probe position in an earlier study of American White Pelicans (Evans 1989). The absence of a significant change in egg center temperature as pipping and hatching proceeded in both studies, despite the significant drop in upper surface temperatures at this time, appears to result from a combination of two effects: (1) the egg center temperature during the pre-

pip stage represents the approximate mid-point of the gradient through the egg from top to bottom, and (2) after pipping, the gradient is absent, as temperatures on all surfaces, upper, lower, and 90°, level out at or just above 35°C. That the latter temperature happens to be the same as the mid-range of the gradient during the pre-pip stage may be fortuitous, but in any event explains why a significant temperature drop at the upper egg surface can occur without being reflected at the egg center. As far as I am aware, the loss of the top-to-bottom temperature gradient with the onset of pipping has not been reported previously, but may be a general phenomenon in species where application of the brood patch to the eggs changes markedly at that time (e.g., Laridae, Beer 1962, Drent 1970).

During the early stages of incubation, avian embryos are small and tend to float to the top of the yolk, and so are positioned close to the upper egg surface (Drent 1970). Subsequently, the enlarging embryo takes up a transverse position adjacent to the air cell near the large end of the egg (Freeman and Vince 1974). Throughout this time, the upper egg surface temperature, and especially that lying towards the blunt end of the egg where the upper surface probe was positioned in these experiments, would correlate closely with the temperature actually attained by the embryo (Drent 1970). An incubation temperature of about 37°C may therefore be a close estimate of the temperature applied to the embryo throughout much, if not most, of the incubation period. Towards the end of the incubation period, when the embryo begins to fill more and more of the egg space, the upper portions of the egg towards the blunt end may still be the most relevant for the embryo, as the relatively inert yolk is concentrated at the lower side of the egg, especially near the small pole (Freeman and Vince 1974), where cooler temperatures would presumably have less of a retarding effect on development. It is relevant that artificial incubation of pelican eggs at the temperature usually used for domestic fowl, 37.8°C, results in a high percentage hatch of viable pelican eggs (Evans 1990).

The abrupt drop in upper surface egg temperature with the onset of pipping and hatching of the a-egg, and a corresponding decrease in the proportion of temperature readings in the "safe" region at or above 36.0°C supports the contention that the terminal, or b-egg in American White Pelicans is potentially subject to some degree of neglect after the a-egg pips. Evans (1990) found that a lowering of incubation temperature by an additional 3°C to 33.0°C during the pipped egg stage caused an increase of over 50% in the pip-to-hatch interval. This suggests that fairly minor amounts of egg cooling due to parental neglect could retard the hatching of b-eggs, causing them to lag farther behind the a-egg. Any increase in hatching asynchrony is potentially damaging to the younger sibling in

species exhibiting a high probability of brood reduction, as in the white pelican (Cash and Evans 1986). Additional manipulative field experiments are required to determine the amount of hatching delay and resultant fitness costs to the terminal egg arising from neglect under natural incubation conditions in this species.

The low b-egg incubation temperatures found in this study are in accord with the prediction that it would be adaptive for parents in brood-reducing species to invest relatively less in terminal offspring. Despite the inherent appeal of such an interpretation, it is important to emphasize that other, possibly non-adaptive interpretations may also account for terminal egg neglect in pelicans. It is possible, for example, that neglect of the b-egg during the final stages of incubation in this species arises because the parent, no longer holding the eggs under its foot webs, lacks adequate information about the true temperature state of the unpipped b-egg, and so is unable to regulate its temperature optimally. This interpretation is consistent with the suggestion (Evans 1988b, 1989; see also Drent 1970 and references), that once the b-egg pips, its vocalizations when cold could have the effect of reinstating normal incubation attentiveness from a cooperative parent. This possibility is under investigation.

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